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Research paper

Xuanweioxylon scalariforme gen. et sp. nov.: Novel Permian coniferophyte stems with scalariform bordered pitting on secondary xylem tracheids

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ABSTRACT

Fossil lignophyte stems show remarkable diversity including non-sympodial and sympodial forms and a variety of pith and tracheid structures. Most lack scalariform bordered pits on radial walls of secondary xylem tracheids, while these occur in the putative progymnosperm *Protopitys* and some (but not all) cycads, bennettitaleans, and angiosperms. We describe a new genus of Permian gymnosperms that comprises decorticated stems and branches with a parenchymatous pith that is septate in stems but entire in branches and has scleroid cells that are organised singly or in bands. Vasculature is non-sympodial, comprising endarch primary xylem strands that become mesarch leaf traces that are occluded through ontogeny. Secondary xylem is pycnoxylic with scalariform bordered pits on radial tracheid walls. The eustelic and non-sympodial organisation, the septate pith and the presence of scalariform bordered pits on secondary tracheids represent a unique combination of features not previously seen in lignophyte genera, justifying the erection of *Xuanweioxylon scalariforme* gen. et sp. nov. *X. scalariforme* shows similarities to several extinct and extant lignophytes but is placed within the coniferophytes — an informal grouping of conifer-like plants of uncertain affinity that includes probable sister groups to cordaitaleans and conifers. Scalariform bordered pitting in secondary tracheids is unique to *Xuanweioxylon* within coniferophytes, demonstrating previously unrecognised diversity within the group. Results suggest that coniferophytes include intermediates between cordaitaleans and conifers with other lignophytes including *Protopitys*, pteridosperms, cycads and Bennettitales.

1. Introduction

Lignophytes are a clade that includes seed plants and their progymnospermous ancestors that are united in having 'gymnospermous' wood produced by a bifacial vascular cambium (Rothwell and Serbet, 1994). They include free-sporing progymnosperms that are either homosporous such as the Aneurophytales, or heterosporous such as the Archaeopteridales and *Cecropsis*, as well as gymnosperms and angiosperms that have attained the reproductive sophistication of the seed (Crane, 1985; Rothwell and Serbet, 1994; Hilton and Bateman, 2006). A diversity of lignophyte stems and branches have been identified that, in general terms, show increasingly complex organisations through the late Palaeozoic (e.g. Galtier, 1992; Galtier and Meyer-Berthaud, 2006) as the clade diversified and adapted to fill different ecological niches. However, the majority of the species and genera are known as isolated organ species (sensu Bateman and Hilton, 2009) or isolated plant fossils (sensu Cleal and Thomas, 2010) rather than whole-plant species from which cladistic relationships have been determined. Coniferophytes are one such example that represent an informally recognised grouping of extinct plants that are conifer-like in their structure but also share features with extinct cordaitaleans (e.g. Rothwell and Mapes, 2001; Serbet et al., 2010). They are typically known as isolated organs rather than fully characterised whole-plants, and are each of uncertain affinity. They may be members of the cordaitaleans or conifers, or they may be closely related sister groups to these. Evolutionary relationships of many potentially important fossil plants such as previously recognised coniferophytes remain poorly understood.

In this study we describe and diagnose a new genus of gymnosperm based on stems preserved from the Lopingian (upper Permian) of South China that we name *Xuanweioxylon scalariforme* gen. et sp. nov. *Xuanweioxylon* is unusual in being non-sympodial with a septate pith, and for possessing scalariform bordered pits in the secondary tracheids. Different combinations of these features occurred in progymnosperms, pteridosperms, cordaitaleans, Palaeozoic conifers, cycads, bennettitaleans and angiosperms. We interpret *Xuanweioxylon*

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to be a coniferophyte. *Xuanweioxylon* shows that coniferophytes were more diverse than previously thought and suggests they include intermediates between cordaitaleans as well as their putative sister group conifers and other lignophyte groups. Non-sympodial architecture and scalariform bordered pits in the secondary xylem tracheids in *Xuanweioxylon* appear to represent primitive features retained from the group's gymnosperm ancestry.

2. Materials and methods

Four decorticated specimens have been recovered from blocks of tuffaceous sediment from the Huopu coal mine in Panxian County of western Guizhou Province, China (Wang et al., 2006). This underground mine extracts coal from the Xuanwei Formation that represent a series of terrestrial, fluvial and deltaic sediments including peat-forming mire deposits and interbedded volcanic tuffs (Wang et al., 2011a). The Xuanwei Formation was deposited during the late Wuchiapingian to Changsingian stages of the Permian Period (Wang et al., 2011a), approximately 260–251 Ma.

The specimens were cut to reveal transverse, longitudinal and tangential sections and then prepared using the acetate peel method (Galtier and Phillips, 1999). Exposed surfaces were etched in 5% HCl leaving the organic contents standing proud of the etched surface and peels were mounted on glass slides with coverslips using Eukitt (O. Kindler GmbH, Freiburg, Germany). The slides were observed and photographed with a Nikon microscope under transmitted light with a Nikon 4500 digital camera. A peel of the secondary xylem was mounted on an SEM stub to examine tracheid structure and analysed uncoated using a HitachiS-4800 Field Emission Scanning Electron Microscope (10.0 KV). Digital images were adjusted for tone and colour balance in Corel PhotoPaint (v. 12), and plates constructed with CorelDraw (v. 12). The specimens and peels containing the specimen are deposited in the Coal Ball Laboratory of the State Key Laboratory of the Systematic and Evolutionary Botany, Institute of Botany, the Chinese Academy of Sciences, Beijing.

3. Systematic palaeobotany

PHYLUM Coniferophyta (Serbet et al., 2010)
GENUS Xuanweioxylon He, Wang, Hilton et Shao *gen. nov.*
Generic diagnosis: Non-sympodial gymnosperm stems with pith, primary and secondary xylem. Pith wide, parenchymatous with sclerotic cells and transfusion tissue, divided into thick-walled peripheral loop and thin-walled central part (with septum or not). Primary xylem strands numerous. Secondary xylem pycnoxylic. Tracheids of the secondary xylem with scalariform bordered pits on radial walls.
Etymology: Derived from the name of the Xuanwei Formation in which the fossils occur, and the greek *oxylon* relating to wood.
Type species: *Xuanweioxylon scalariforme* He, Wang, Hilton et Shao gen. et sp. nov.
Holotypus hic designatus: HP2007-2a

Several peels and thin sections were prepared from the single stem selected as the holotype (specimen HP2007-2a). The peels are numbered HP2007-2 (Plate I, 4), N-L-9 (Plate III, 1). The thin sections are numbered WP2L-0076 (Plate I, 1, 5; Plate II, 7–9, 11; Plate III, 3, 5), WP2L-0077 (Plate I, 2, 3; Plate II, 1, 3, 4, and 6; Plate III, 7; Plate IV, 1–3), WP2L-0082 (Plate I, 6; Plate II, 2, 12), WP2-0127 (Plate II, 5, 10; Plate III, 2, 9; Plate IV, 6–10), WP2-0128 (Plate III, 4, 6, 8, 10, and 11; Plate IV, 11, 13), WP2-0130 (Plate IV, 12).
Paratypes: HP2007-2b, HP2007-2c, HP2007-2d

The thin sections of HP2007-2b are numbered WP2-0085 (Plate V, 1–3, 5, 7, and 8), WP2-0177 (Plate V, 4, 9, and 10), WP2-0178 (Plate V, 6). The thin section of HP2007-2c is numbered WP2-0083 (Plate V, 11). HP2007-2d is not shown in the plates.
Repository: Coal Ball Laboratory of the State Key Laboratory of the Systematic and Evolutionary Botany, Institute of Botany, the Chinese Academy of Sciences, Beijing.
Collecting locality: Huopu coal mine in Panxian County of western Guizhou Province, China (Wang et al., 2006).
Stratigraphic position and age: Xuanwei Formation, late Wuchiapingian to Changshingian stages, Lopingian series, Permian period (Wang et al., 2011a).
Etymology: Referring to the distinctive tracheids with scalariform bordered pits present in the secondary xylem.
Specific diagnosis: Wood without growth rings. Pith septate in big stems and entire in smaller ones. Peripheral loop composed of continuous and radially elongated thick-walled parenchyma cells. Scleroid cells in bands or single at the outer margin adjacent to the primary xylem. Secretory canals occasionally at the periphery of the pith. Central septate part composed of isodiametrical parenchyma cells. Primary xylem strands c. 50 in number. Leaf traces occluded after a few millimetres. Phyllotaxy helical. Pits on radial tracheid walls of secondary xylem uniseriate, scalariform bordered, horizontal and not in contact with tangential tracheid walls. Cross-field showing 1–2 large, oval or nearly round simple pits, or several small oculipores. Rays 1–19 cells high, uniseriate or partly biseriate (about 20%), much denser, shorter and wider near the pith than those at the periphery.

4. Description

4.1. General features

Observations come from four stems that have well-preserved pith and xylem but are decorticated. The majority of information comes from the largest specimen (stem A) which is described first (Plates I to IV), with observations then augmented by information from stems B (Plate V, 1–10) and C (Plate V, 11) that are smaller; stem D is a small twig but it is poorly preserved and does not provide any additional information to that identified from the other specimens. Transverse section of stem A (Plate I, 1–2) is slightly oval in transverse section, 28 × 32 mm in diameter, and 105 mm long, stem B is elliptical in transverse section, 10 × 25 mm in diameter (Plate V, 1), and stem C is smaller, approximately 14 × 9 mm in diameter (Plate V, 11). The stem is non-sympodial and possesses a parenchymatous pith that is septate in larger specimens (Plate I, 4, 6) and entire in smaller ones (Plate V, 4, 6), with sclerotic cells singly and as bands surrounding the xylem (Plate I, 5; Plate II, 1; Plate V, 6–7), and transfusion tissue (Plate II, 7, 11; Plate V, 8). Primary xylem strands are in contact with the secondary xylem (Plate II, 4; Plate III, 1), numerous (Plate I, 3; Fig. 1), distinct and endarch at their origin (Plate III, 1, 3), but become mesarch as they pass outwards through the stem where they become leaf traces and occluded in secondary xylem (Plate III, 7, 9–10). Secondary xylem is well-developed, lacks growth rings and is pycnoxylic with uniseriate rays (Plate IV, 1, 12), or partly biseriate (c. 20%). Tracheids of the secondary xylem have scalariform bordered pits on the radial walls (Plate IV, 3–5). Each cross-field has 1–2 large, oval or nearly round simple pits, or several small oculipores with a narrow, slit-like and almost horizontal opening (Plate IV, 8–10).

4.2. Pith

The pith is slightly oval in cross section (Plate I, 1–3), 12 × 15 mm in diameter, and is divided into the peripheral loop (medullary sheath) and central septate part in transverse section depending on the cell type, extension direction and vertical continuity (Plate I, 3–6). Cells of the peripheral loop are continuous vertically (Plate I, 4, 6). The width of the loop varies in transverse section between different areas and in different parts of the same loop, and is between 0.5 and 2.5 mm (Plate I, 1–3). At the periphery of the loop, and in contact with the xylem, occur irregularly and closely packed scleroid cells in zones (Plate I, 3, 5–6; Plate II, 1–4). Scleroid cells are nearly isodiametric in transverse and radial sections, c. 25–70 μm in diameter

(Plate II, 1–2); the wall is thick and dark-coloured but is typically poorly preserved. Scleroid cells form weak bands in some areas (Plate II, 3) and these are interrupted by the primary xylem (Plate II, 4). Inner part (side) of the loop comprises of thick-walled parenchyma cells, most of them are radially elongated, oval or polygonal (Plate II, 3–5). Small lacunae occur in these cell walls (Plate II, 6) and some cells have reticulate thickening on each wall (Plate II, 7) or septum (Plate II, 3). Cell diameter increases gradually from the outside where they are typically c. 55 × 50–70 × 110 μm to the inner part where they are c. 50 × 110–80 × 190 μm. Cell walls are typically c. 3–4 μm thick, though they can be relatively thinner and lighter coloured (Plate II, 4). Secretory canals are occasionally present at the periphery of the loop (Plate II, 8).

The central septate part of the pith possesses the septae and parenchyma cells that occur between adjacent septa (Plate I, 3, 4, and 6). Parenchyma cells become destroyed to form a cavity in some places (Plate I, 3, 4, and 6). The thickness of the diaphragm varies widely from 2 to 5.5 mm and is narrowest at the midpoint, widening gradually to the margin (Plate I, 6). Individual pith septa may furcate vertically (Plate I, 4). The diaphragm consists of parenchyma cells that are isodiametric in transverse section (Plate II, 9) and elongated horizontally in radial section (Plate II, 10). Cell walls are usually light brown to buff coloured and have reticulate thickening (Plate II, 11) and septum (Plate II, 9); these cells are frequently broken, leaving adjacent cell walls attached to one another (Plate II, 9, 12). Parenchyma cells in the middle of this zone are typically c. 80 × 80–140 × 230 μm in diameter and are larger than those at the margin that are typically from 60 × 60 to 95 × 160 μm in diameter. The parenchyma cells between the diaphragm may not be the same as those in the diaphragms as they vary considerably in size and shape, including round, oval, rhomboid and polygonal forms (Plate II, 5, 12). Cells in this part of the pith always have dark contents and a cavity.

4.3. Primary xylem

The eustele possesses c. 50 discrete primary xylem strands with the endarch maturation (Fig. 1; Plate I, 3; Plate III, 1). Primary xylem strands are triangular with a blunt top in transverse section (Plate III, 1). Metaxylem tracheids have annular to scalariform thickenings on all walls (Plate III, 2). Following primary xylem strands continuously through cross-sections, it is apparent that all of primary xylem strands are leaf traces on different levels; there are no cauline vascular bundles and thus the primary vascular system of the stem consists of only leaf traces and is non-sympodial. Leaf traces originate at the inner margin of the secondary xylem and are very small making observations difficult (Plate II, 1), but become more obvious as they go up (Plate III, 3) and develop centripetal metaxylem and become mesarch. On the upper level, leaf traces divide to form double traces (Plate III, 5) and both extend out into the secondary xylem (Plate III, 6–7), but a minority of the leaf traces may divide to form 3–4 vascular bundles (Plate III, 8). In each cross section through the stem, 3–4 leaf traces can be observed (Plate I, 1–2), with all leaf traces extending c. 3.3 mm before they are occluded in the secondary xylem (Plate III, 9–10). Leaf traces are helically arranged in tangential section (Plate III, 11).

Plate I. Stems of *Xuanweioxylon scalariforme* He, Wang, Hilton et Shao gen. et sp. nov. All figures of the holotype, 1–3 and 5 are in transverse section, 4 and 6 are in tangential section. Scale bars = 3 mm unless otherwise stated.

1. Stem with a broad pith (P) and secondary xylem (SX), five leaf traces (LT), and narrow peripheral loop (PL). Slide WP2L-0076.
2. Inner part of stem showing inner septate pith (IS) and peripheral loop. Slide WP2L-0077.
3. Enlargement of pith from Pl. I, 2 showing c. 50 primary xylem bundles (arrows). Slide WP2L-0077.
4. Pith with developed septum with thick diaphragms. Pith dichotomies may be irregularly (white arrow), and large lacuna are present (black arrow). Scale bar = 5 mm, Peel HP2007-2 AR.
5. Enlargement of Pl. I, 1 showing parenchyma cells of the peripheral loop with scleroid cells (SC) and inner septate part of pith with diaphragm (D). Scale bar = 500 μm. Slide WP2L-0076.
6. Detail of pith and cavity between diaphragms (arrows). Slide WP2L-0082.

Plate II. *Xuanweioxylon scalariforme* He, Wang, Hilton et Shao gen. et sp. nov. All figures of the holotype; 1, 3–4, 6–9 and 11 are in transverse section, others are in tangential section. 9–12 show parenchyma of inner septate part of pith. (see on page 156)

1. Scleroid cells and interrupted at primary xylem. Scale bar = 100 μm, Slide WP2L-0077.
2. Scleroid cells with thick walls. Scale bar = 30 μm, Slide WP2L-0082.
3. Periphery loop with thick-walled parenchyma cells and scleroid cells with weak area (arrow) at the outside-edge, diaphragm on parenchyma cell walls (D). Scale bar = 500 μm, Slide WP2L-0077.
4. Peripheral loop with thin- and thick-walled parenchyma cells, scleroid cells and primary xylem (PX). Scale bar = 500 μm, Slide WP2L-0077.
5. Radially elongate parenchyma cells of peripheral loop (PL), septum (S) and cells of the inter septum (InS). Scale bar = 100 μm, Slide WP2-0127.
6. Thick-walled parenchyma cells of the peripheral loop with round pits (arrow) in the wall. Scale bar = 50 μm, Slide WP2L-0077.
7. Parenchyma cells with reticulate pits. Scale bar = 100 μm, Slide WP2L-0076.
8. Secretory canal at the periphery of the pith. Scale bar = 100 μm, Slide WP2L-0076.
9. Many parenchyma cells only with residual cell wall (white arrow), diaphragm on cell walls (black arrow). Scale bar = 500 μm, Slide WP2L-0076.
10. Parenchyma cells radially elongate in radial section. Scale bar = 200 μm, Slide WP2-0127.
11. Cells with dark content and reticulate pits. Scale bar = 30 μm, Slide WP2L-0076.
12. Septum with residual cell walls(S) and inter septum part (InS) with isodiametric parenchyma cells. Scale = 500 μm, Slide WP2L-0082.

Plate III. Primary xylem and leaf traces of *Xuanweioxylon scalariforme* He, Wang, Hilton et Shao gen. et sp. nov. All figures of the holotype. 1, 3, 5, 7 and 8 are traverse sections, 2 and 9 are radial, and others are tangential. (see on page 157)

1. Five small primary xylem bundles (arrows), pith (P) and secondary xylem (SX). Scale bar = 1 mm, Peel N-L-9.
2. Primary xylem tracheids with scalariform and reticulate pits and pith (P). Scale bar = 100 μm, Slide WP2-0127.
3. Primary xylem bundle showing endarch maturation. Scale bar = 100 μm, Slide WP2L-0076.
4. Double leaf traces not yet separate in tangential section. Scale bar = 500 μm, Slide WP2-0128.
5. Leaf trace branches to mesarch double leaf traces near the pith. Scale bar = 100 μm, Slide WP2L-0076.
6. Double leaf traces in tangential section. Scale bar = 500 μm, Slide WP2-0128.
7. Double leaf traces in secondary xylem. Scale bar = 500 μm, Slide WP2L-0077.
8. Four leaf traces in secondary xylem. Scale bar = 500 μm, Slide WP2-0128.
9. Primary xylem adjacent to pith expanding outwards at an angle (arrow, bottom) and leaf trace expanding outwards horizontally (arrow, top) in secondary xylem. Scale bar = 3 mm, Slide WP2-0127.
10. Disruption of traces disappears as leaf trace disappears in secondary xylem. Scale bar = 500 μm. Slide WP2-0128.
11. Leaf traces showing helical arrangement in tangential section. Scale bar = 3 mm, Slide WP2-0128.

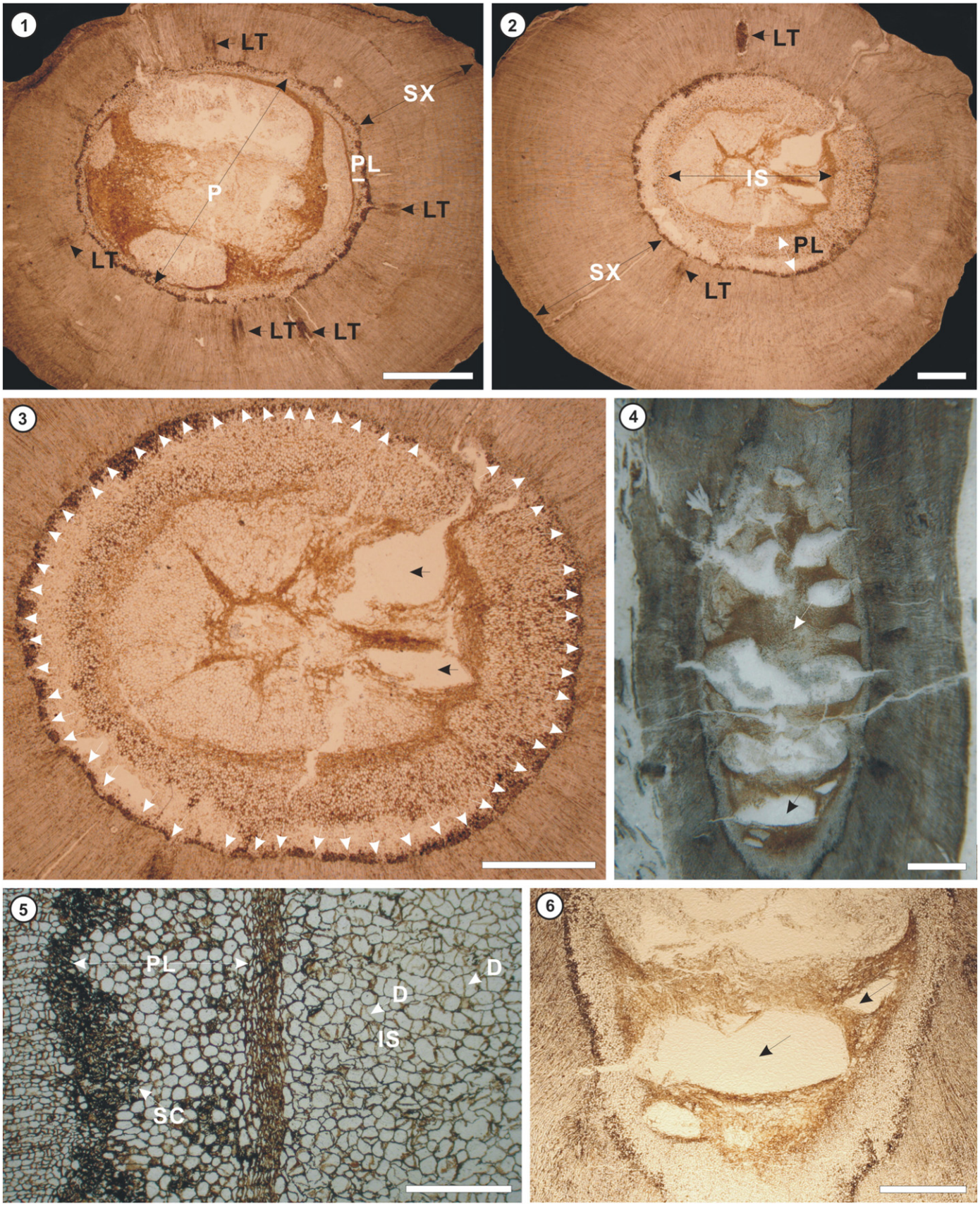

Plate I.

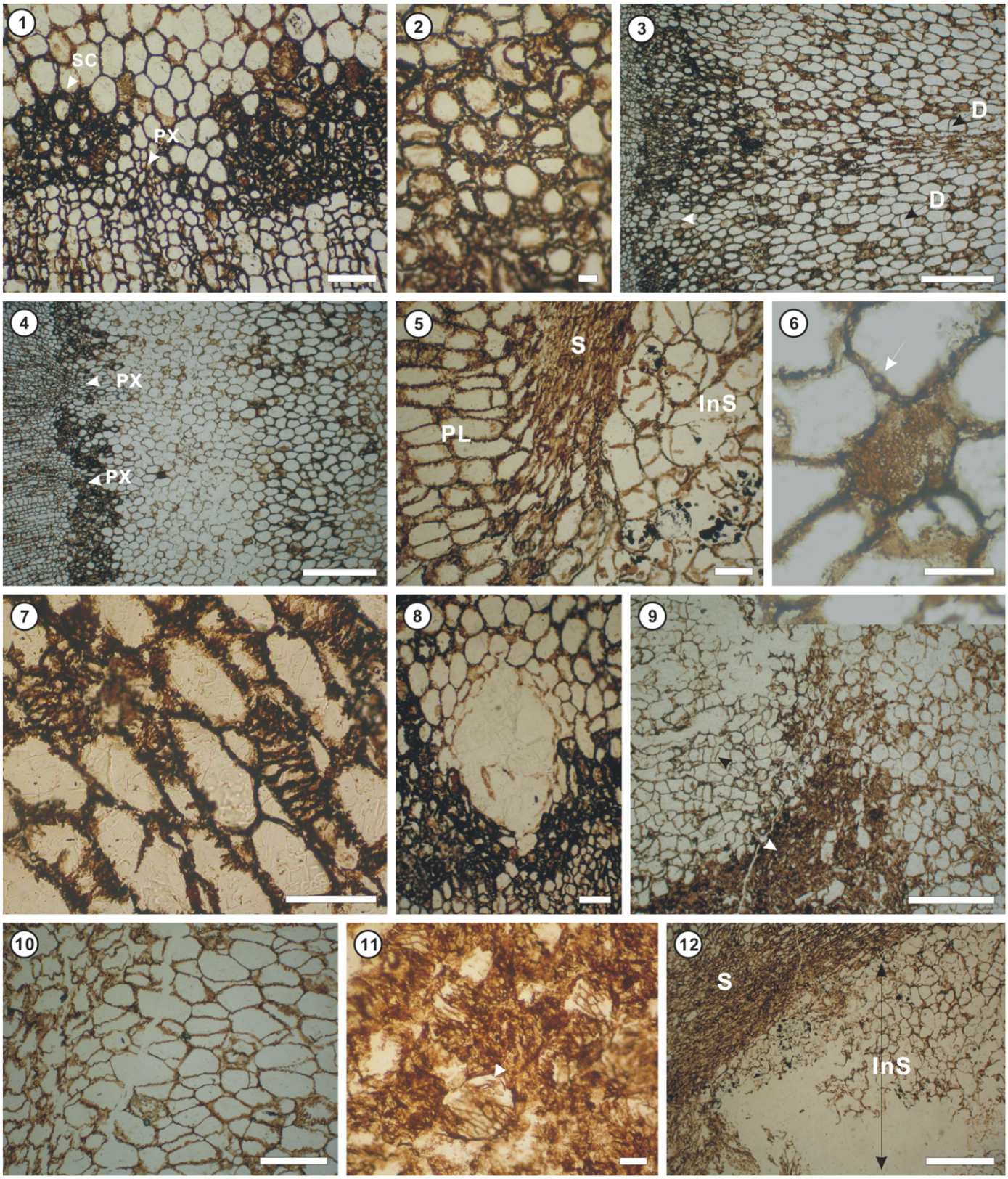

Plate II (*caption on page 154*).

4.4. Secondary xylem

Secondary xylem is pycnoxylic and consists of tracheids and rays (Plate IV, 1–2). Tracheids are square to rectangular with radial dimensions wider than tangential (Plate IV, 1), or square to flat with radial width less than the tangential one in cross section (Plate IV, 2). Tracheids vary from 20 × 25 to 36 × 55 μm in cross section, their walls c. 1–2.5 μm thick and often slightly bent. Rays are usually uniseriate at the periphery (Plate IV, 1), becoming wider toward the pith (Plate IV, 2), so partly biseriate rays are not unusual near the pith. Ray cells are

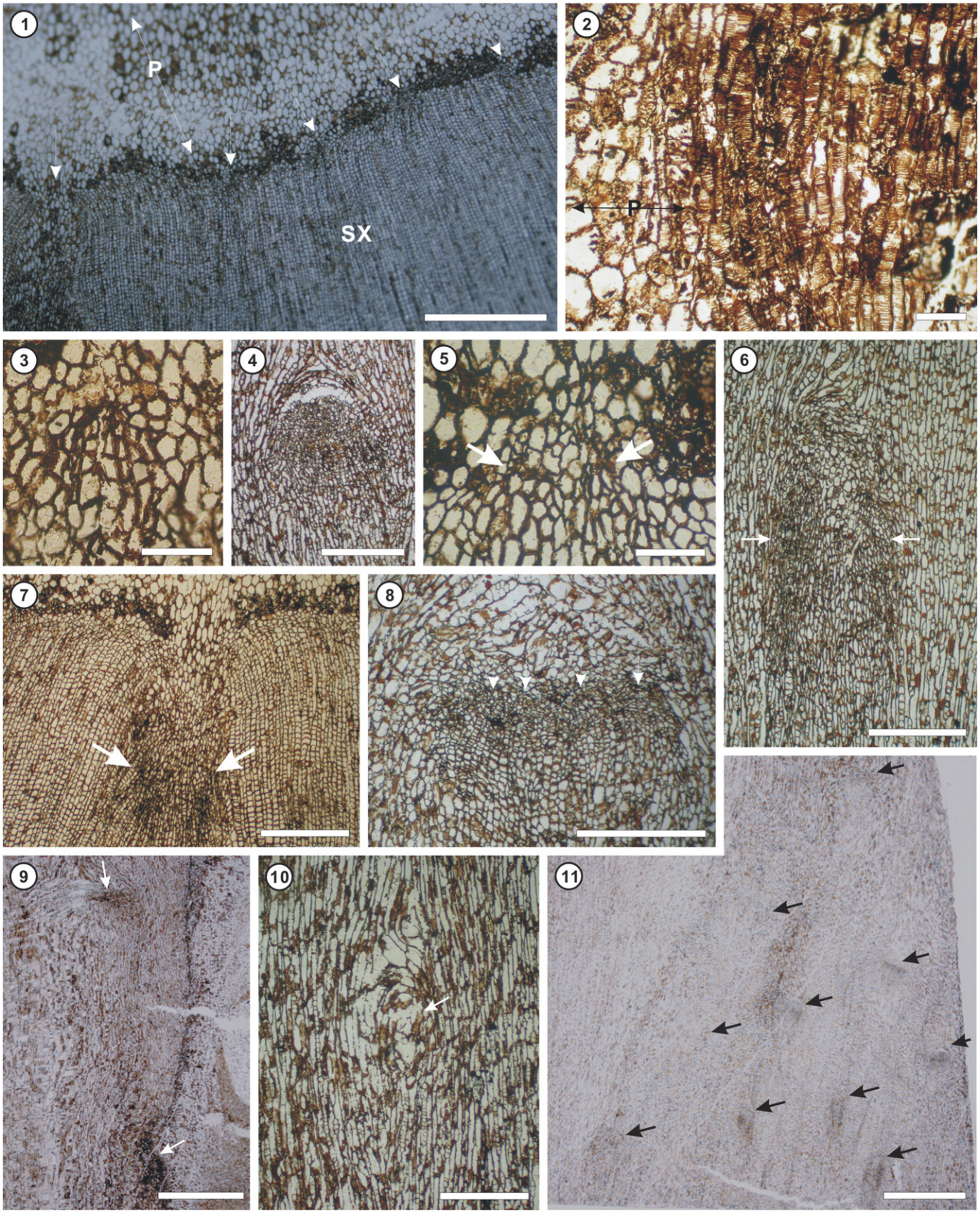

Plate III (*caption on page 154*).

parenchymatous and rectangular to nearly oval, c. 75–225 μm in radial direction and c. 18–35 μm in tangential direction at the periphery, whereas they become shorter and wider toward the pith, and measure c. 30–80 μm in radial direction and c. 25–45 μm in tangential direction, which makes the rays somewhat expanded toward to the pith. The density of rays is higher near the pith where there are 9–10 rays per mm^2 (Plate IV, 2) and lower at the periphery where there are 3–9 rays per mm^2 (Plate IV, 1).

In the radial section, pits on the radial tracheid walls are uniseriate and scalariform bordered, positioned in the middle axial part of the tracheid, covering only about 2/3 to 2/5 of total tracheid width (Plate IV, 3–5). Scalariform bordered pits vary from c. 13 to 23 μm (typically 15–20 μm) wide and c. 5–7 μm high. Occasionally on radial walls pits are round, either uniseriate or weakly biseriate alternated (Plate IV, 6–7). Rays are unified with similar parenchyma cells and stems lack axial parenchyma; ray parenchyma cells are rectangular with thin walls, their tangential walls are vertical or slightly oblique while horizontal walls are smooth and often slightly bent (Plate IV, 8). Cross-field areas show each 1–2 large oval or nearly round simple pits (may be as a result of alteration) from 15 × 20 to 18 × 22 μm in diameter (Plate IV, 8–9), or several small oculipores with a narrow slit-like and almost horizontal opening (Plate IV, 10). Leaf traces extend out at an angle near the pith then become almost horizontal in the secondary xylem, and all of the leaf traces are occluded after a few millimetres (Plate III, 9).

In the tangential section, tracheid walls are straight, but tracheids may bend. Tracheid end walls are often apiculate, intrusive or even divided (Plate IV, 11). The single tracheids vary irregularly from 1.4 to 1.9 mm in length with a mean length of 1.6 mm. Tangential walls lack ornamentation, rays are uniseriate or partly biseriate (c. 20%) and rays near the pith are much denser and shorter than those at the periphery (Plate IV, 12–13; Fig. 2). Near the pith, rays are 1–17 (typically 1–4) cells high (mean = 3.56; n = 200); single ray cells are large, their height greater than their widths, typically c. 25–45 μm (mean = 35.8 μm) high and c. 18–40 μm (mean = 26.6 μm) wide. Rays of the periphery are relatively sparse and are higher than those near the pith. Single rays may be high, varying from 1 to 19 cells (typically 1–8) high (mean = 5.37; n = 200); single cells are relatively small and are wider than they are high, c. 16–45 μm (mean = 28.1 μm) high and c. 20–35 μm (mean = 29.7 μm) wide.

4.5. Stems B and C

The pith of specimen B is 4 × 16 mm in diameter, parenchymatous and lacks developed septum (Plate V, 1), and is divided into central part and peripheral loop by a cycle of parenchyma cells which only have remnants of cell walls (Plate V, 1–4). There are about 1–5 layers small and isodiametric parenchyma cells at the peripheral edge of the loop, 35–50 μm in diameter (Plate V, 3). Parenchyma cells in the peripheral loop are radially arranged (Plate V, 2), and several scleroid cells are scattered in this loop (Plate V, 4–7). The central part is solid with continuous isodiametric parenchyma cells, without obvious diaphragms (Plate V, 3, 6). Reticulate thickened parenchyma cells often appear in the pith (Plate V, 8). The eustele does not have cauline vascular bundles and consists of c. 50 discrete endarch primary xylem strands (Plate V, 1, 3). Primary xylem strands bifurcate to double leaf traces and turn to mesarch (Plate V, 2), and extend out into secondary xylem. The secondary xylem is pycnoxylic, the tracheids have uniseriate scalariform bordered pits on radial walls (Plate V, 9). Rays are uniseriate or partly biseriate (Plate V, 10). Stem C is a twig which possesses well-preserved pith, part primary xylem strands and secondary xylem (Plate V, 11). The pith possesses parenchyma cells, some cells with reticulate thickenings. The cells of the periphery are radially arranged compared to those in the centre that are isodiametric. This specimen lacks sclerotic cells. Primary xylem strands are endarch and secondary xylem is pycnoxylic.

5. Discussion

5.1. Comparison of stems A–D

The stems and branches described here co-occur in the same assemblage and have consistent features that allow us to consider them as a single species. Of the four stems, A is the largest and we interpret this as a mature stem with developed pith septae in which leaf traces have been occluded and leaves abscised. Specimen A is the designated holotype. Stem B is younger and has not developed the

Plate IV. Secondary xylem of *Xuanweioxylon scalariforme* He, Wang, Hilton et Shao gen. et sp. nov. All figures of the secondary xylem of the holotype; 1–2 are traverse sections, 3–9 are radial, and 10–12 are tangential sections.

1. Secondary xylem at the stem periphery showing neatly arranged tracheids and narrow rays. Scale bar = 100 μm, Slide WP2L-0077.
2. Secondary xylem adjacent to pith showing dense and wider rays. Scale bar = 100 μm, Slide WP2L-0077.
3. Scalariform bordered pits on secondary tracheid radial walls. Scale bar = 100 μm, Slide WP2-0127.
4. SEM image showing uniseriate scalariform bordered pits. Scale bar = 15 μm.
5. SEM image showing uniseriate scalariform bordered pits. Scale bar = 20 μm.
6. Biseriate alternated scalariform pits on radial tracheid walls. Scale bar = 30 μm.
7. Uniseriate nearly round pits on secondary xylem tracheids radial walls. Scale bar = 30 μm, Slide WP2-0127.
8. Ray parenchyma cells in radial section and large pits on tracheids (bottom). Scale bar = 100 μm, Slide P2-0127.
9. Large single pits in cross-field. Scale bar = 30 μm, Slide WP2-0127.
10. Four nearly round alternated oculipores with a narrow opening in cross field. Scale bar = 30 μm, Slide WP2-0127.
11. Tracheids diverge at end. Scale bar = 100 μm, Slide WP2-0128.
12. Sparce and high rays at the periphery of secondary xylem. Scale bar = 100 μm, Slide WP2-0130.
13. Dense, uniseriate or partly biseriate rays near the pith margin. Scale bar = 100 μm, Slide WP2-0128.

Plate V. *Xuanweioxylon scalariforme* He, Wang, Hilton et Shao gen. et sp. nov. 1–10 are stem B, 11 is stem C; 1–3, 5, 7–8 and 11 are traverse section, 4, 6 and 9 are radial sections, 10 is tangential section. (see on page 160)

1. Axis with a wide pith and xylem, pith divided to peripheral loop (PL) and inter septate part (IS) by a ring of parenchyma cells (A). Scale bar = 3 mm. Slide WP2-0085.
2. Enlargement of the pith from Pl. V, 1 showing double leaf trace (LT), peripheral loop (PL) with radially elongated parenchyma cells and inner septate part of pith (IS). Scale bar = 500 μm. Slide WP2-0085.
3. Dense endarch primary xylem bundles and small parenchyma cells in pith adjacent to xylem. Scale bar = 500 μm. Slide WP2-0085.
4. Parenchymatous pith divided by annulus (A). Scale bar = 500 μm. Slide WP2-0177-1.
5. Scleroid cells intrude to secondary xylem following the leaf trace. Scale bar = 500 μm. Slide WP2-0085.
6. Scleroid cells in pith. Scale bar = 500 μm. Slide WP2-0178.
7. Scleroid cells in pith. Scale bar = 100 μm. Slide WP2-0085.
8. Parenchyma cells of pith with reticulate pits. Scale bar = 30 μm. Slide WP2-0085.
9. Scalariform bordered pitting on secondary xylem radial tracheid walls and radially elongated ray cells. Scale bar = 30 μm. Slide WP2-0177-1.
10. Uniseriate, low and dense rays. Scale bar = 500 μm. Slide WP2-0177-2.
11. Axis of stem C with pith and part secondary xylem. Scale bar = 3 mm, Slide WP2-0083.

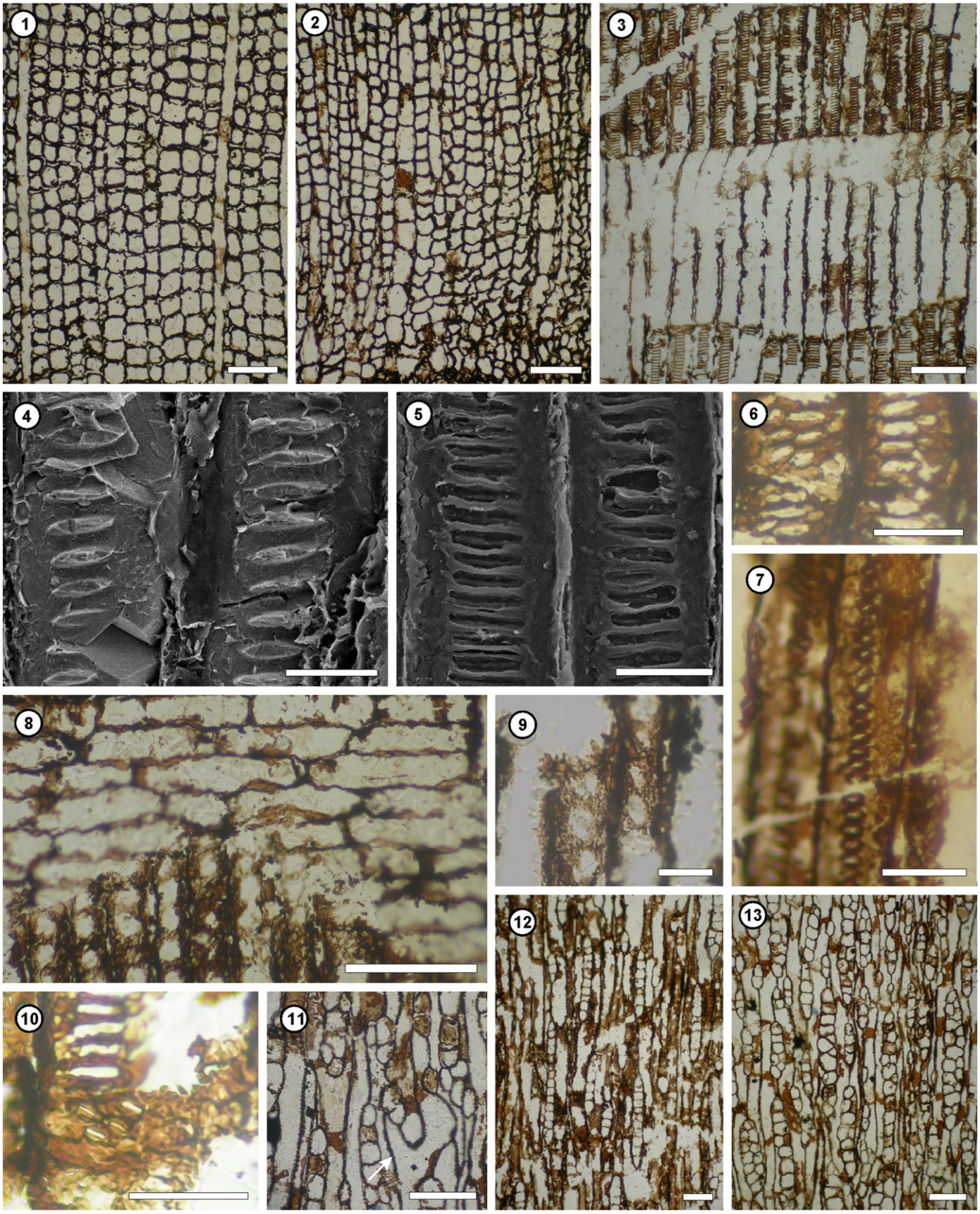

Plate IV.

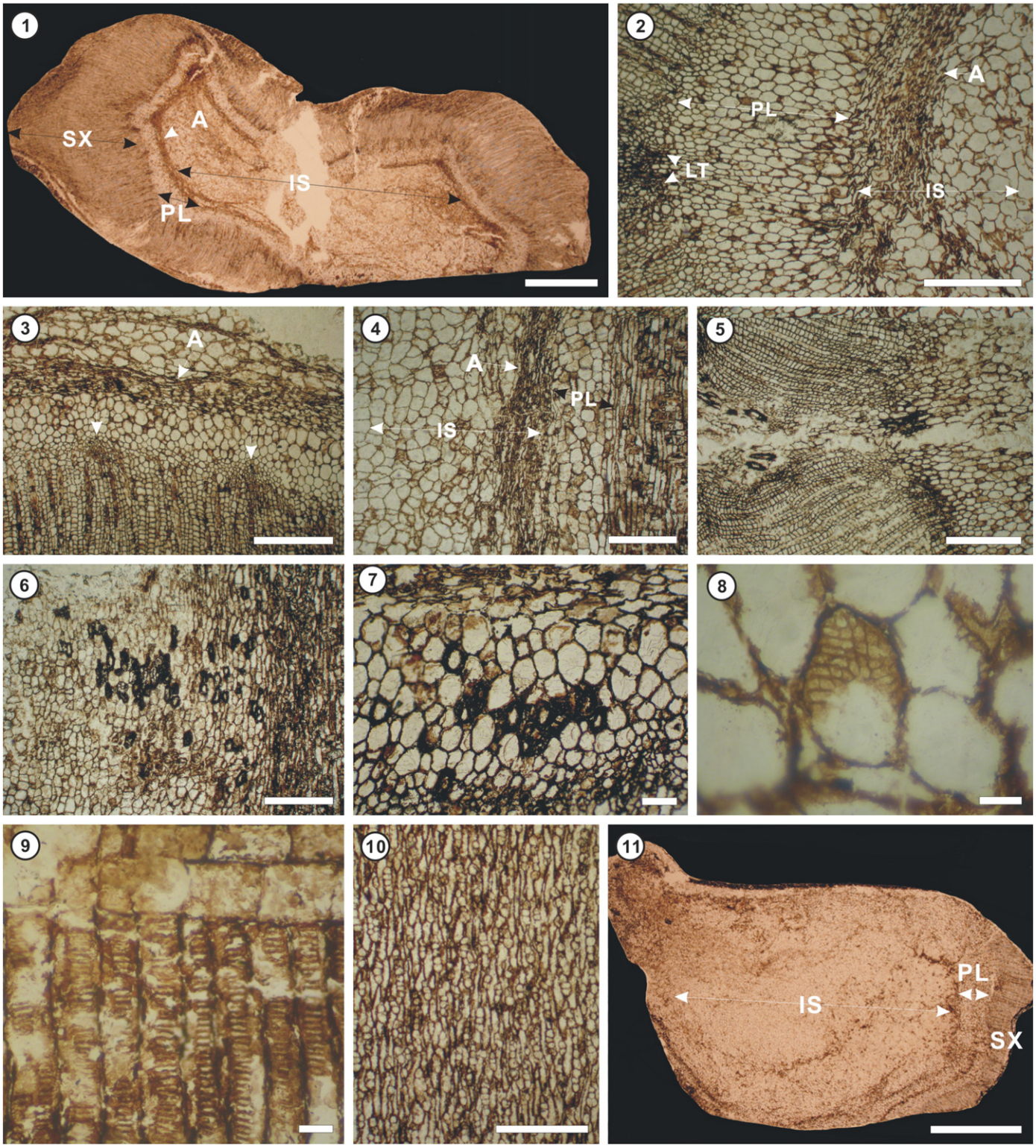

Plate V (*caption on page 158*).

horizontal pith septae seen in stem A, and its leaf traces have not been occluded through ontogeny. In stem B scattered sclerotic cells in the pith are far less frequent than those in stem A, and in stem B they occur away from the sclerotic loop rather than around the pith margin as they do in stem A. We conclude that the differences of stems B and A represent different developmental stages or different parts of the same species. Stem C is the smallest and is a twig, and in this pith septa or sclerotic cells have not developed. Stem D (not figured) is broadly similar to Stem B but is not well preserved and provided no additional information. We therefore consider these co-occurring specimens to represent a single fossil species.

5.2. Comparisons and affinity

Xuanweioxylon shares anatomical features with a range of lignophytes making its affinity difficult to interpret. Among progymnosperms,

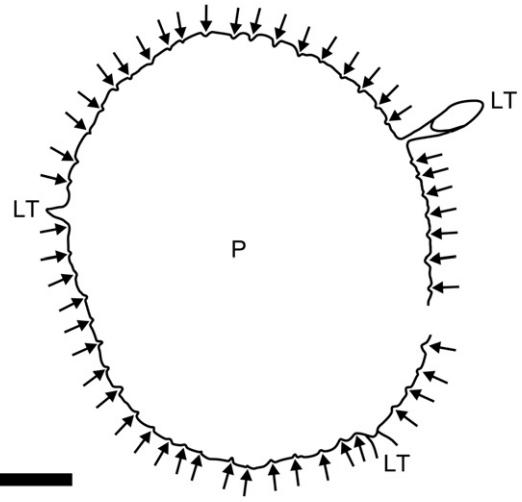

Fig. 1. Camera-lucida diagram of outer margin of pith (P) showing position of leaf traces (LT) and primary xylem bundles (arrows) of *Xuanweioxylon scalariforme* He, Wang, Hilton, et Shao gen. et sp. nov. Scale bar = 3 mm, Slide WP2-0077.

scalariform bordered pitting on the secondary xylem tracheid radial walls only appears in *Protopitys buchiana* Goeppert (Galtier et al., 1998). Although widely accepted as a progymnosperm, we consider the affinity of *Protopitys* less certain as it may represent the male organs of a basal pteridospem for which ovulate organs have yet to be discovered; we therefore consider *Protopitys* to be a putative progymnosperm rather than a proven member of this group. *Protopitys buchiana* possesses endarch primary xylem and pycnoxylic secondary wood and has uniseriate or biseriate scalariform bordered pitting restricted to radial tracheid walls. In *P. buchiana*, rays are uniseriate and low, and the species lacks or has subtle growth rings, while its pith is elliptical in transverse section and a pair of protoxylem poles occur at opposite ends of the pith (Walton, 1957); protoxylem strands divide to form an arc-shaped trace that is emitted from the side of the stele. This is different from stems of *Xuanweioxylon* that has a round pith with well-developed pith septae, and has many more but singly smaller leaf traces. In transverse section, the tracheid size is also smaller in *Xuanweioxylon*. As a group, Progymnosperms range from the Eifelian stage of the Devonian to the Tournaisian stage of the Mississippian (Beck and Wight, 1988), with existing evidence demonstrating progymnosperms become extinct approximately 90 million years before the Lopingian occurrence of *Xuanweioxylon*. We conclude *Xuanweioxylon* is not a progymnosperm.

Among late Palaeozoic pteridosperms, the arborescent genera *Eristophyton*, *Bilignea*, *Stanwoodia* and *Endoxylon* have stems with a broad pith, a eustele and pycnoxylic secondary xylem (Galtier and Meyer-Berthaud, 2006). Pteridosperms have been documented lacking scalariform pitting on secondary xylem tracheid walls and lack pith diaphragms (Stewart and Rothwell, 1993; Galtier and Meyer-Berthaud, 2006) with the exception of *Megaloxylon scottii* (Seward, 1917; Mapes, 1985). Although *Megaloxylon* has a septate pith, the pith is larger in *Xuanweioxylon* and *Megaloxylon* typically has 5–6 large leaf traces (Seward, 1917; Mapes, 1985) unlike the c. 50 small ones in *Xuanweioxylon*. In *Megaloxylon* rays are wider, and *Megaloxylon* is further differentiated from *Xuanweioxylon* by its multiseriate bordered pits on the tracheids of the secondary xylem (Seward, 1917; Mapes, 1985). In general, ray heights and widths are greater in pteridosperms, as are tracheid sizes (Galtier, 1988, 1992; Galtier and Meyer-Berthaud, 2006). We conclude that *Xuanweioxylon* is not a pteridosperm.

Stems of the cordaitealean *Mesoxylon* share with *Xuanweioxylon* a broad, round pith with parenchyma cells and well-developed pith diaphragms, discrete primary xylems and non-sympodial cauline vascular bundles, and pycnoxylic secondary xylem. In *Mesoxylon priapi*, the primary xylem strands are almost impossible to distinguish from the innermost cells of secondary xylem adjacent to the pith, as they are in *Xuanweioxylon*. However, within cordaitaleans, secretory canals only rarely appear at the periphery medulla in species of *Shanxioxylon* (Wang et al., 2003b, 2009), but isolated or bands of scleroid cells seen in the pith of *Xuanweioxylon* are unknown. In the pith of *Shanxioxylon sinense* (Wang et al., 2003b), *Cordaixylon tianii* (Wang et al., 2009) and *Cordaixylon* sp. of Falcon-Lang (2007), thin-walled parenchyma cells occasionally have small round pits, but these lack the scalariform bordered pits. There are several major differences between stems of *Xuanweioxylon* and cordaitaleans including the number of the primary xylem strands where there are c. 50 in *Xuanweioxylon* and c. 35 in cordaitaleans. Moreover, in cordaitaleans the primary xylem and early (innermost) secondary xylem tracheids show scalariform thickening rather than pitting, whilst the outer tracheids have circular pits, rather than scalariform bordered pitting on radial walls. Also, the pith diaphragm is very thick and irregularly branched in *Xuanweioxylon* compared to the *Artisia*-type of cordaitaleans that are thin and have nearly horizontal diaphragms.

Pith 'secretory' or 'sclerotic' nests are common in extinct and extant conifers (Doubinger and Marguerier, 1975; Galtier et al., 1992) and also occur in *Xuanweioxylon*. *Xuanweioxylon* and conifers have thick, branched pith septae with scleroid cells in the pith, and they are also similar in their pith, pycnoxylic wood with uniseriate rays, small leaf traces (Galtier et al., 1992; Rothwell et al., 2005). *Xuanweioxylon* differs from conifers in its non-sympodial organisation and in the presence of scalariform bordered pits.

Cycads have transfusion tissue and scleroid cells in a wide pith, and have numerous primary xylem strands and scalariform pits. *Xuanweioxylon* differs from cycads in having a septate pith, in having small leaf traces that are occluded through ontogeny, in possessing pycnoxylic wood with uniseriate rays, and in having uniseriate to weakly biseriate rather than its multiseriate pits in secondary xylem tracheid radial walls (Artabe et al., 2005; Wang et al., 2011b).

Although of unknown systematic affinity, stems and leaves of gigantopterids occur in the Xuanwei Formation. Stems of *Aculeovinea guizhouensis* (Li and Taylor, 1998) and *Vasovinea tianii* (Li and Taylor,

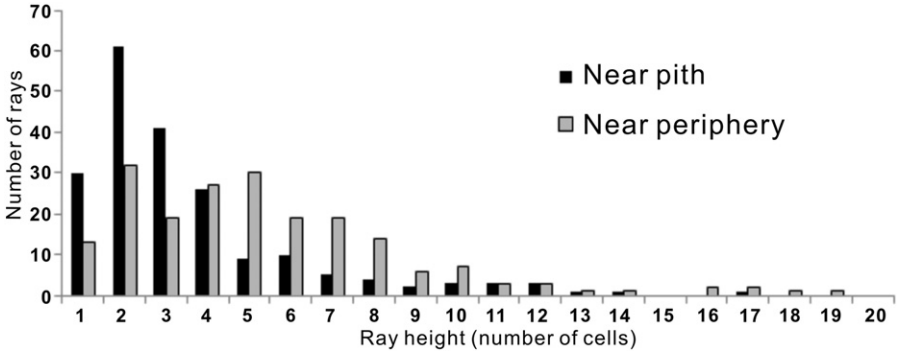

Fig. 2. Histogram showing frequency distribution or ray height measured in number of cells from 200 rays in tangential longitudinal section in *Xuanweioxylon scalariforme*.

1999) are small, typically 1–2 cm in diameter and comprise fewer but larger primary xylem strands, weakly developed secondary xylem with wide (up to 4 cells) and tall (up to 70 cells) rays. The overall features of these gigantopterids are quite different from those of *Xuanweioxylon* and we conclude that *Xanweioxulon* is not a gigantoperid.

From the Xuanwei Formation and the contemporaneous Longtan Formation in Guizhou Province, gymnosperm stems of *Guizhouoxylon dahebianense* (Tian and Li, 1992) and *Walchiopremnon gaoi* (Tian et al., 1994) have been previously reported. *Walchiopremnon gaoi* is different from *Xuanweioxylon* in having secretory cells in the pith, isodiametric bordered pits on radial walls of secondary xylem tracheids and wide rays in the secondary xylem. The pith in *Xuanweioxylon* differs from that in *G. dahebianense*; the latter is much smaller (only 5 mm), irregular in shape, continuous and contains vertically elongate secretory cells with black contents, the early-formed secondary xylem tracheids are conspicuously larger than the late-formed ones. *Xuanweioxylon* is very different from these species.

In summary, *Xuanweioxylon* has a unique combination of features seen in other lignophyte groups but has the greatest similarity with extinct cordaitealeans and conifers but does not readily conform to either of these groups. The differences noted above distinguish *Xuanweioxylon* from all other plant genera for which we establish *Xuanweioxylon scalariforme* He, Wang, Hilton et Shao gen. et sp. nov. to accommodate it. We consider *Xuanweioxylon* to be a coniferophyte of uncertain systematic affinity but presumably closely related and potentially sister group to cordaitaleans or conifers, and note similarities and potential intermediate structure with other lignophyte groups including cycads and Bennettittales.

5.3. Pith

Mature stems of *Xuanweioxylon* possess a thick pith that is parenchymatous with well-developed septae, while younger stems are parenchyatous and lack septae. Among pycnoxylic lignophytes, pith septa are common in Palaeozoic cordaitaleans (Rothwell, 1988) and some early conifers (Rothwell et al., 2005; Hernandez-Castillo et al., 2009), and are absent in progymsperms, cycads and *Ginkgo*, and most (but not all) pteridosperms. Some manoxylic pteridosperms were irregularly septate including *Glossopteris skaarensis* (Pigg and Taylor, 1993) and *Eoguptioxylon* (Crisafulli and Lutz, 2007), while the pith of the *Megaloxylon scottii* bears superficial resemblance to the septate pith of cordaitaleans (Seward, 1917, fig. 448B).

Cordaitaleans have pith diaphragms of the *Artisia*-type (Rothwell, 1988) with the exception of *Mesoxylon priapi* (and perhaps *M. birame*) that has a parenchymatous pith and *Piracicaboxylon meloi* that has a parenchymatous ring (Rothwell, 1988; Taylor et al., 2009). The septate pith of voltzialean conifers, such as *Walchiopremnon* (Tian et al., 1994), *Barthelia* (Rothwell and Mapes, 2001; Rothwell et al., 2005) and *Emporia* (Hernandez-Castillo et al., 2009), sometimes become irregularly ruptured as the stem elongated, but not in the same way as seen in the cordaitalean *Cordaixylon* (Florin, 1951; Stewart and Rothwell, 1993). *Tylodendron* is a genus for fossil pith casts with longitudinal furrows, presumably of early conifers (Noll and Wilde, 2002), and *Artisia* comprises pith casts with horizontal septae belonging to cordaitaleans. Apart from the voltzialean conifers, some other early conifers including *Scleromedulloxylon* (Doubinger and Marguerier, 1975), *Septomedullopitys* (Lepechina, 1972) and *Solenoxylon* (Kräusel, 1956) also had an irregular septate pith.

In cordaitaleans, *Artisia*-type pith septa were produced when the branch elongated and caused some of the pith cells to break down (Stewart and Rothwell, 1993). By contrast, in voltzialean and other early conifers, *Tylodendron*-type pith septa are always irregularly ruptured with distinct longitudinal striations, and unlike cordaitaleans, they often have sclerotic cells in the diaphragms. *Artisia*-type casts do not show distinct longitudinal striations because the irregular primary xylem of cordaitaleans scarcely formed wedges (Noll and Wilde, 2002). Overall, the pith of *Xuanweioxylon* is more like that of Palaeozoic conifers in being irregularly ruptured but in conifers it is formed by sclerenchyma and in *Xuanweioxylon* is formed by transfusion tissue (see below), while in cordaitaleans it is formed from the parenchyma.

5.4. Transfusion tissue

In the pith of *Xuanweioxylon*, many thick-walled parenchyma cells exhibit reticular thickenings on the cell walls that are tracheid-like. These are distributed as single cells throughout the pith and are surrounded by normal, thick-walled parenchyma cells; they do not form tracheids. We consider these to be transfusion cells or tissues (e.g. Greguss, 1968, 1969) that are likely to have functioned in the storage and short distance transport of water (Kucera, 1977).

Transfusion cells in gymnosperm leaves and in the pith of extant cycads comprise thin-walled parenchyma cells (Griffith, 1957; Greguss, 1969). In living cycads, transfusion tissue is present in a number of different forms where it is used to distinguish species (e.g. Greguss, 1968), and in some fossil cycads such as *Lioxylon liaoningense* (Zhang et al., 2006) is distributed at the pith periphery. Within the Cupressaceae, transfusion tissue is common in the pith of *Taxus* and *Cephalotaxus* (Kucera, 1977), and it also occurs frequently within pteridosperms as pitted parenchyma cells such as *Bilignea* (Scott, 1924), *Megaloxylon* (Mapes, 1985), *Stanwoodia* (Galtier and Scott, 1991), and in the unusual gymnosperm shoot *Cladites* (Scott, 1930). Among cordaitaleans, *Shanxioxylon sinense* (Wang et al., 2003b) and *Cordaixylon tianii* (Wang et al., 2009) occasionally have several parenchyma cells with small single pits distributed within the pith, and in some species of *Cordaixylon* can occur as round pits in the pith cells (Falcon-Lang, 2007). The pith of the extinct ginkgophyte *Palaeoginkgoxylon zhoui* (Feng et al., 2010) has vertically aligned pitted parenchymatous cells. Reticulate pitting in pith parenchyma is not limited to gymnosperms and has been reported in the lycopsid such as *Diaphorodendron vasculare* (Binney) DiMichele (*Lepidodendron vasculare* as figured in Hirmer, 1927, fig. 248) whereas round pits have been observed in some species of calamite (Wang et al., 2003a). The distribution of reticulate pitting in pith parenchyma in different gymnosperm groups are likely to have originated more than once and are likely to represent modified pith elements that have no obvious phylogenetic significance. Transfusion tissue in the pith of the coniferophyte *Xuanweioxylon* is very different from that cordaitaleans and conifers but is more similar with some pteridosperms as well as more derived gymnosperms including cycads and bennettitaleans.

5.5. Scleroid cells and secretory canals at the periphery pith

The pith of *Xuanweioxylon* has sclereids distributed as single cells and bands of cells at the outer margin of the pith. Pith 'secretory' or 'sclerotic' nests have not previously been reported in cordaitaleans (Rothwell, 1988) but in stems of *Shanxioxylon taiyuanense* secretory canals occur at the periphery of the pith (Hilton et al., 2009; Wang et al., 2009). In extinct and extant conifers, secretory or sclerotic nests are common (Doubinger and Marguerier, 1975; Galtier et al., 1992). In this regard the coniferophyte *Xuanweioxylon* is more conifer-like than cordaitalean-like.

5.6. Primary xylem system

Phyllotaxy and the underlying vascular pattern of a plant may change during ontogeny and this is well-documented within various plant groups including conifers and dicotyledonous angiosperms (Beck et al., 1982). Vascular structure has been considered to be among the most conservative of vegetative features in plant evolution and represents an important criterion for the delimitation of plant groups (e.g. Florin, 1951; Rothwell, 1976; Wang, 1997). In *Xuanweioxylon*, the

stem is eustelic and comprises of c. 50 discrete endarch primary xylem strands that are initially small and difficult to distinguish from the secondary xylem. Stems of *Cordaixylon* (Stewart and Rothwell, 1993) have primary xylem strands that are also small and difficult to distinguish from the innermost cells of the secondary xylem adjacent to the pith, but cordaitalean stems typically have c. 30 primary xylem strands. Pteridosperm stems with more xylem strands include *Cauloxylon* and *Megalomyelon* (Cribbs, 1939, 1940) that have c. 100 strands.

The primary xylem of eustelic progymnosperms, most arborescent pteridosperms, *Gingko*, conifers and cycads all consist of numerous sympodial xylem strands (Rothwell, 1976; Beck et al., 1982; Rothwell, 1982; Galtier and Meyer-Berthaud, 2006), whereas stems of *Xuanweioxylon* are non-sympodial and lack cauline vascular bundles. Within gymnosperms non-sympodial organisation occurs within the Devonian pteridosperm *Elkinsia* (Serbet and Rothwell, 1992), and the Carboniferous pteridopsperms *Eristophyton feistii* (Decombeix et al., 2008), *E. waltonii* (Lacey, 1953; Galtier and Scott, 1991), *Bilignea* (Galtier and Scott, 1994) and species of *Heterangium* including *H. sturii*, *H. kukukii* and *H. lintonii* (Kubart, 1914; Stidd, 1979). Stems of *Heterangium* are manoxylic and protostelic, and protoxylem groups in this genus are only delimited when they begin to leave the stele as leaf traces. Cordaitaleans include sympodial taxa such as *Cordaixylon* and *Shanxioxylon* as well as non-sympodial taxa including species of *Mesoxylon* including *M. multirame*, *M. sutcliffii*, *M. platypodium*, and *M. priapi* (Whiteside, 1974; Rothwell, 1988; Wang, 1997). Within dicotyledonous angiosperms, Benzing (1967a,b) determined that c. 1/3 of species, all of them woody ranaleans, lacked sympodia. However, according to Beck et al. (1982), the evidence thus far presented on sympodial distribution in angiosperms does not eliminate the possibility that some of these species have sympodial systems (Beck et al., 1982).

All previously reported non-sympodial gymnosperm fossils have been found in the Palaeozoic and include the basal members of the seed plant clade in current understanding of seed plant relationships (e.g. Rothwell and Serbet, 1994; Hilton and Bateman, 2006) where it appears to represent the symplesiomorphic condition. Within cordaitaleans, the non-sympodial genus *Mesoxylon* has been interpreted as a primitive member of the group (Wang, 1997) with the more derived and stratigraphically younger species being sympodial. If lacking sympodia is correctly interpreted as plesiomorphic within pteridosperms and cordaitaleans, the stratigraphically late occurrence of the non-sympodial coniferophyte stem *Xuanweioxylon* from the Permian of China is unusual and appears to have retained this primitive feature from its pteridosperm ancestry as it has in *Mesoxylon*.

5.7. Secondary xylem

Stems of *Xuanweioxylon* have well-developed pycnoxylic secondary xylem. Several putative arborescent pteridsperms are pycnoxylic including *Bilignea*, *Stanwoodia*, *Endoxylon* and *Eristophyton* that are each known as decorticated stems (Lacey, 1953; Galtier, 1988; Galtier and Meyer-Berthaud, 2006). Secondary xylem in *Xuanweioxylon* has uniseriate or partly biseriate low rays and neatly arranged small tracheids that are very similar as those of cordaitaleans and conifers, but are dissimilar from those in pycnoxylic pteridosperms that have taller and mutiseriate rays and bigger tracheids.

Scalariform elements are characteristic of many pteridophytes and also occur in the progymnosperm *Rellimia* (Leclercq and Bonamo, 1971) and the putative progymnosperm *Protopitys buchiana* (Walton, 1957; Galtier et al., 1998), but is less common within seed plants (Beck, 2010). However, during the Palaeozoic only *Protopitys buchiana* (Walton, 1957; Galtier et al., 1998) and *Xuanweioxylon* have scalariform bordered pits in secondary xylem tracheids. Cordaitaleans and some pteridosperms only have metaxylem and first formed secondary xylem composed of scalariform tracheids (Stewart and Rothwell, 1993). A notable exception is *Johnhallia lacunosa*, a pteridosperm from the middle Pennsylvanian of Indiana that has both scalariform and multiseriate rows of bordered pits on radial walls of the secondary xylem (Stidd and Phillips, 1982). Cribbs (1935) described "*Cordaites*" *missouriense* from the Mississippian of North America as cordaitalean wood with oblong pitting in the secondary tracheid radial walls, but the affinity of this is uncertain as only the secondary xylem is known in this species. *Cladites bracteatus* has scalariform pits on secondary xylem tracheids (Scott, 1930), but the affinity of this species is of unknown (Galtier, 1997) from which we consider it may represent the fertile shoot of a presently unknown coniferophyte.

Scalariform pitting occurs in the Mesozoic wood *Scalaroxylon* (Vogellehner, 1967) where it is common on the radial walls. Approximately five Mesozoic wood genera have homoxylous tracheids with at least some scalariform pitting, namely *Paradoxoxylon*, *Ecpagloxylon*, *Sahnioxylon*, *Phoroxylon* and *Lhassoxylon* (Philippe et al., 2010), but for each the affinity is unknown. Scalariform pits are normally absent from the secondary xylem in *Ginkgo* and conifers except *Agathis borrtensis* where they occur in cross-fields (Thomson, 1914). Scalariform pitting and bordered pits are also common in extant (Greguss, 1968) and extinct cycads including *Michelilloa* (Artabe et al., 2005) and *Antarcticycas* (Smoot et al., 1985), and are widespread within bennettitaleans (e.g. Saiki and Yoshida, 1999). Some Gnetales including *Gnetum* (Muhammad and Sattler, 1982) and species of dicotolyedonous angiosperms (including *Trochodendron*, *Tetracentron* and *Tasmannia*) with "homoxylous" wood that lacks vessels have secondary xylem tracheids with scalariform bordered pits (Stewart and Rothwell, 1993).

Previous studies have considered scalariform pits to represent a primitive condition within seed plants with circular pits evolving from scalariform pits, and with reticulate pits as a transitory stage (e.g. Stewart and Rothwell, 1993; Beck, 2010). Vessels are thought to have evolved from tracheids with scalariform lateral pitting similar to those of several of the primitive vesselless dicotyledons (Beck, 2010). Based on observations of scalariform pits in the primary xylem and initially produced secondary xylem in pteridosperms and cordaitaleans, Takhtajan (1976) suggested that scalariform pitting in cycads, cycadeoids and angiosperms is an extrapolation of the juvenile feature of scalariform pitting in the metaxylem into the secondary xylem. Whatever the origin, scalariform bordered pitting in secondary xylem tracheids of *Xuanweioxylon* is unusual within coniferophytes and may link the group with the putative progymnosperm *Protopitys* and Mesozoic conifers.

5.8. Leaf traces

Like *Xuanweioxylon*, other Palaeozoic gymnosperms have endarch primary xylem strands that divide to form two mesarch leaf traces including *Cauloxylon* (Cribbs, 1939) and *Eristophyton waltonii* (Lacey, 1953). Leaf traces arise from the periphery of the pith at an angle and extend outwards nearly horizontally through the secondary xylem as they do in *Mesoxylon thompsonii* (see fig. 16 of Traverse, 1950). One leaf trace in *Xuanweioxylon* branches twice to produce four vascular bundles in the secondary xylem, and all of the leaf traces are occluded after about 3.3 mm within the secondary xylem; this also occurs within arborescent pycnoxylic pteridosperms (Galtier and Meyer-Berthaud, 2006) as well as some cordaitaleans including *Mesoxylon thompsonii* (Traverse, 1950) and *Mesoxylon* sp. of Falcon-Lang et al. (2011). Occlusion of leaf traces but without growth rings in *Xuanweioxylon* shows that leaves persisted for more than one year and shed as the stem matured with the plant being deciduous. This suggests that *Xuanweioxylon* was evergreen and inhabited a non-seasonal habitat, but identify of the leaves of the *Xuanweioxylon* plant are unknown at present. Deciduousness has been considered to be an innovation character in Palaeozoic seed plant evolution (e.g. Galtier and Meyer-Berthaud, 2006) but is common in cordaitaleans and conifers, and presumably coniferophytes such as *Xuanweioxylon*.

5.9. Ecology

During the Permian the tectonic block that forms modern day South China was located near the equator in a tropic–subtropical zone and hosted a seasonal rain-forest with humid and temperate climate (Tian and Zhang, 1980; Shen, 1995; Tian and Wang, 1995). *Xuanweioxylon* possessed deciduous leaves on mature stems, but shows no evidence of seasonal growth interruption such as growth rings. Leaf traces in the secondary xylem are very similar to those of evergreen conifers and angiosperms, but it is uncertain if *Xuanweioxylon* was evergreen with leaves abscised after more than one growth season.

The flora of the Xuanwei Formation is diverse and dominated by marattialean ferns, sphenopsids and seed plants, but also includes plants of more enigmatic affinities including gigantopterids, taeniopterids and noeggerathialeans (Zhao et al., 1980). Seed plants include pteridosperms, cycads including *Pterophyllum*, *Nilsonia*, the putative cycad *Plagiozamites*, and the conifer *Ullmania* sp. (Tian and Zhang, 1980; Zhao et al., 1980). Lycopsids are present but infrequent within the formation. Palaeoenvironments from the Xuanwei Formation include terrestrial, fluvial, peat-forming mires and deltaic facies (Wang et al., 2011a) from which we conclude that the preserved flora preserves plants from more than one environmental setting. In the Xuanwei Formation mire-dwelling elements included lycopsids and sphenopsids, while marattialeans, pteridosperms, cycads, taeniopterids and gigantopterids probably lived in habitats surrounding the mires, while conifers appear to represent upland elements. Stems of *Xuanweioxylon* occur as clasts within tuffaceous conglomerates alongside well-rounded clasts of basic igneous rock in a medium-coarse grained feldspathic matrix. We interpret this sediment to represent either a high energy fluvial deposit eroding freshly formed igneous rocks, or a proximal volcaniclastic lahar (P. J. Windslow, J. Hilton and L. Shao, manuscript in progress). This lithology lacks typical wetland plants seen elsewhere in the formation and appears to preserve parts of an upland or extra-basinal flora; we interpret *Xuanweioxylon* to have been adapted for living in an upland environment and was transported by volcanic processes into lowland depositional settings.

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References

Artabe, A.E., Zamuner, A.B., Stevenson, D.W., 2005. A new genus of Late Cretaceous cycad stem from Argentina, with reappraisal of known forms. Alcheringa 29, 87–100.
Bateman, R.M., Hilton, J., 2009. Palaeobotanical systematics for the phylogenetic age: applying organ-species, form-species and phylogenetic species concepts in a framework of reconstructed fossil and extant whole-plants. Taxon 58, 1254–1280.
Beck, C.B., 2010. An Introduction to Plant Structure and Development: Plant Anatomy for the Twenty-first Century, Second edition. Cambridge University Press, Cambridge.
Beck, C.B., Wight, D.C., 1988. Progymnosperms. In: Beck, C.B. (Ed.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 1–84.
Beck, C.B., Schmid, R., Rothwell, G.W., 1982. Stelar Morphology and the Primary Vascular System of Seed Plants. The Botanical Review 48, 691–815.
Benzing, D.H., 1967a. Developmental patterns in stem primary xylem of woody Ranales. I. Species with unilacunar nodes. American Journal of Botany 54, 805–813.
Benzing, D.H., 1967b. Developmental patterns in stem primary xylem of woody Ranales. II. Species with trilacunar and multilacunar nodes. American Journal of Botany 54, 813–820.
Cleal, C.J., Thomas, B.A., 2010. Botanical nomenclature and plant fossils. Taxon 59, 261–268.
Crane, P.R., 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Annals of the Missouri Botanical Garden 72, 716–793.
Cribbs, J.E., 1935. *Cordaites missouriense* from the Lower Carboniferous of Missouri. American Journal of Botany 22, 427–438.
Cribbs, J.E., 1939. *Cauloxylon ambiguum*, gen. et sp. nov., a new fossil plant from the Reed Springs Formation of Southwestern Missouri. American Journal of Botany 26, 440–449.
Cribbs, J.E., 1940. Structure of fossil stem of Pityan affinity from the Reed Springs Formation of Missouri. Botanical Gazette 101, 582–597.
Crisafulli, A., Lutz, A., 2007. *Eoguptioxylon antique* gen. et sp. nov. (Pteridospermae) from the Upper Permian La Antigua Formation, La Rioja Province, Argentina. Ameghiniana 44, 197–204.
Decombeix, A.-L., Meyer-Berthaud, B., Galtier, J., 2008. Diversity of Mississippian arborescent lignophytes: a new species of *Eristophyton* from the middle Tournaisian of France. International Journal of Plant Sciences 169, 1116–1127.
Doubinger, J., Marguerier, J., 1975. Paléoxylologie: Étude anatomique comparée de *Scleromedulloxylon aveyronense*nov. gen. nov. sp. du Permien de St-Affrique (Aveyron, France); considérations taxinomiques et stratigraphiques. Geobios 8, 25–59.
Falcon-Lang, H.J., 2007. A *Cordaixylon* axis from well-drained alluvial plain facies in the Lower Pennsylvanian Joggins Formation of Nova Scotia. Atlantic Geology 43, 87–90.
Falcon-Lang, H.J., Jud, N.A., Nelson, W.J., DiMichele, W.A., Chaney, D.S., Lucas, S.G., 2011. Pennsylvanian coniferopsid forests in sabkha facies reveal nature of seasonal tropical biome. Geology 39, 371–374.
Feng, Z., Wang, J., Roessler, R., 2010. *Palaeoginkgoxylon zhoui*, a new ginkgophyte wood from the Guadalupian (Permian) of China and its evolutionary significance. Review of Palaeobotany and Palynology 162, 146–158.
Florin, R., 1951. Evolution in cordaites and conifers. Acta Horti Bergiani 15, 285–388.
Galtier, J., 1988. Morphology and phylogenetic relationships of early pteridosperms. In: Beck, C.B. (Ed.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 135–176.
Galtier, J., 1992. On the earliest arborescent gymnosperms. Courier Forschungsinstitut Senckenberg 147, 119–125.
Galtier, J., 1997. Coal-ball floras of the Namurian–Westphalian of Europe. Review of Palaeobotany and Palynology 95, 51–72.
Galtier, J., Meyer-Berthaud, B., 2006. The diversification of early arborescent seed ferns. The Journal of the Torrey Botanical Society 133, 7–19.
Galtier, J., Phillips, T.L., 1999. The acetate peel technique. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society of London, London, pp. 67–71.
Galtier, J., Scott, A.C., 1991. *Stanwoodia*, a new genus of probable early gymnosperms from the Dinantian of East Kirkton, Scotland. Transactions of the Royal Society of Edinburgh, Earth Sciences 82, 113–123.
Galtier, J., Scott, A.C., 1994. Arborescent gymnosperms from the Visean of East Kirkton, West-Lothian, Scotland. Transactions of the Royal Society of Edinburgh, Earth Sciences 84, 261–266.
Galtier, J., Scott, A.C., Powell, J.H., Glover, B.W., Waters, C.N., 1992. Anatomically preserved conifer-like stems from the Upper Carboniferous of England. Proceedings of the Royal Society of London B 247, 211–214.
Galtier, J., Schneider, J.L., Grauvogel-Stamm, L., 1998. Arborescent gymnosperms and the occurrence of *Protopitys* from the Lower Carboniferous of the Vosges, France. Review of Palaeobotany and Palynology 99, 203–215.
Greguss, P., 1968. Xylotomy of the Living Cycads with a Description of their Leaves and Epidermis. Akademiai Kiadó, Budapest (255 pp.).
Greguss, P., 1969. Transfusion tissue in the stems of cycads. Phytomorphology 19, 34–43.
Griffith, M.M., 1957. Foliar ontogeny in *Podocarpus macrophyllus*, with special reference to transfusion tissue. American Journal of Botany 44, 705–715.
Hernandez-Castillo, G.R., Stockey, R.A., Mapes, G., Rothwell, G.W., 2009. Reconstruction of the Pennsylvanian-age walchian conifer *Emporia cryptica* sp. nov. (Emporiaceae: Voltziales). Review of Palaeobotany and Palynology 157, 218–237.
Hilton, J., Bateman, R.M., 2006. Pteridosperms are the backbone of seed–plant phylogeny. The Journal of the Torrey Botanical Society 133, 119–168.
Hilton, J., Wang, S.J., Galtier, J., Bateman, R.M., 2009. Cordaitalean seed plants from the early Permian of North China. III. Reconstruction of the Shanxioxylon taiyuanense plant. International Journal of Plant Sciences 170, 951–967.
Hirmer, M., 1927. Handbuch der Paläobotanik, vol. I. Oldenbourg, München, Germany.
Kräusel, R., 1956. Der "Versteinerte Wald" im Kaokoveld, Südwest-Afrika. Senckenbergia. Lethaia 37, 411–445.
Kubart, B., 1914. Über die Cycadofilicineen *Heterangium* und *Lyginodendron* aus dem Ostrauer Kohlenbecken. Österreichische Botanische Zeitschrift 64, 8–19.
Kucera, L.J., 1977. Tracheoids in the pith of Yew (*Taxus baccata* L.). IAWA Bulletin 4, 67–70.
Lacey, W.S., 1953. Scottish Lower Carboniferous plants: *Eristophyton waltoni* sp. nov. and *Endoxylon zonatum* (Kidst.) Scott from Dumbartonshire. Annals of Botany 17, 579–596.
Leclercq, S., Bonamo, P.M., 1971. A study of the fructification of *Milleria* (*Protopteridium*) from the Middle Devonian of Belgium. Palaeontographica Abteilung B 136, 83–114.
Lepechina, V., 1972. Woods of Palaeozoic pycnoxylic gymnosperms with special reference to North Eurasia representatives. Palaeontographica Abteilung B 138, 44–106.
Li, H.Q., Taylor, D.W., 1998. *Aculeovinea yunguiensis* gen. et sp. nov. (Gigantopteridales), a new taxon of gigantopterid stem from the Upper Permian of Guizhou Province, China. International Journal of Plant Sciences 159, 1023–1033.

Li, H.Q., Taylor, D.W., 1999. Vessel-bearing stems of *Vasovinea tianii* gen. et sp. nov., (Gigantopteridales) from the Upper Permian of Guizhou Province, China. American Journal of Botany 86, 1563–1575.
Mapes, G., 1985. *Megaloxylon* in mid-continent North America. Botanical Gazette 146, 157–167.
Muhammad, A.F., Sattler, R., 1982. Vessel structure of *Gnetum* and the origin of angiosperms. American Journal of Botany 69, 1004–1021.
Noll, R., Wilde, V., 2002. Conifers form the "uplands"-petrified wood from central Germany. In: Dernbach, U., Tidwell, D. (Eds.), Secrets of Petrified Plants. D'ORO Publishers, Heppenheim, Germany, pp. 83–103.
Philippe, M., Cuny, G., Bashforth, A., 2010. *Ecpagloxylon mathiesenii* gen. nov. et sp. nov., a Jurassic wood from Greenland with several primitive angiosperm features. Plant Systematics and Evolution 287, 153–165.
Pigg, K.B., Taylor, T.N., 1993. Anatomically preserved *Glossopteris* stems with attached leaves from the central Transantarctic Mountains, Antarctica. American Journal of Botany 80, 500–516.
Rothwell, G.W., 1976. Primary vasculature and gymnosperm systematic. Review of Palaeobotany and Palynology 22, 193–206.
Rothwell, G.W., 1982. New interpretations of the earliest conifers. Review of Palaeobotany and Palynology 37, 7–28.
Rothwell, G.W., 1988. Cordaitales. In: Beck, C.B. (Ed.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 273–297.
Rothwell, G.W., Mapes, G., 2001. *Barthelia furcata* gen. et sp. nov., with a review of Paleozoic coniferophytes and a discussion of coniferophyte systematics. International Journal of Plant Sciences 162, 637–667.
Rothwell, G.W., Serbet, R., 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. Systematic Botany 19, 443–482.
Rothwell, G.W., Mapes, G., Hernandez-Castillo, G.R., 2005. *Hanskerpia* gen. nov. and phylogenetic relationships among the most ancient conifers (Voltziales). Taxon 54, 733–750.
Saiki, K., Yoshida, Y., 1999. A new Bennettitalean trunk with unilacunar five-trace nodal structure from the Upper Cretaceous of Hokkaido, Japan. American Journal of Botany 86, 326–332.
Scott, D.H., 1924. Fossil plants of the *Calamopitys* type from the Carboniferous rocks of Scotland. Transactions of the Royal Society of Edinburgh 53, 569–596.
Scott, D.H., 1930. *Cladites bracteatus*, a petrified shoot from the lower coal-measures. Annals of Botany 44, 333–348.
Serbet, R., Rothwell, G.W., 1992. Characterizing the most primitive seed ferns. 1. A reconstruction of *Elkinsia polymorpha*. International Journal of Plant Sciences 153, 602–621.
Serbet, R., Escapa, I., Taylor, T.N., Taylor, E.L., Cuneo, N.R., 2010. Additional observations on the enigmatic Permian plant *Buriadia* and implications on early coniferophyte evolution. Review of Palaeobotany and Palynology 161, 168–178.
Seward, A.C., 1917. Fossil Plants. III. Pteridospermeae, Cycadofilices, Codaitales, Cycadophyta. Cambridge University Press, Cambridge, UK.
Shen, G.L., 1995. Permian floras, In: Li, X.X. (Ed.), Fossil Floras of China Through the Geological Ages, English edition. Guangdong Science and Technology, Guangzhou, China, pp. 127–223.
Smoot, E.L., Taylor, T.N., Delevoryas, T.N., 1985. Structurally preserved plants from Antarctica.1. *Antarticycas*, gen. nov., a Triassic cycad stem from the Beardmore Glacier Area. American Journal of Botany 72, 1410–1423.
Stewart, W.N., Rothwell, G.W., 1993. Paleobotany and the Evolution of Plants, Second edition. Cambridge University Press, Cambridge.
Stidd, B.M., 1979. A new species of *Heterangium* from the Illinois Basin of North America. Review of Palaeobotany and Palynology 28, 249–257.
Stidd, B.M., Phillips, T.L., 1982. *Johnhallia lacunosa* gen. et sp. n.: a new pteridosperm from the Middle Pennsylvanian of Indiana. Journal of Paleontology 56, 1093–1102.
Takhtajan, A.L., 1976. Neoteny and the origin of flowering plants. In: Beck, C.B. (Ed.), Origin and Early Evolution of Angiosperms. Columbia University Press, New York, pp. 207–219.
Taylor, T.N., Taylor, E.L., Krings, M., 2009. The Biology and Evolution of Fossil Plants, Second edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.
Thomson, R.B., 1914. On the comparative anatomy and affinities of the Araucarineae. Philosophical Transactions of the Royal Society of London 204B (1–50 and pls.1–7).
Tian, B.L., Li, H.Q., 1992. A new specialized stem, *Guizhouoxylon dahebianense* gen. et sp. nov., from Upper Permian in Shuicheng district, Guizhou, China. Acta Palaeobotanica Sinica 31, 336–345.
Tian, B.L., Wang, S.J., 1995. Palaeozoic coal ball floras in China, In: Li, X.X. (Ed.), Fossil Floras of China through the geological ages, English edition. Guangdong Science and Technology, Guangzhou, China, pp. 202–211.
Tian, B.L., Zhang, L.W., 1980. Fossil atlas of Wangjiazhai Mine Region in Shuicheng, Guizhou Province. China Coal Industry Publishing House, Beijing (in Chinese).
Tian, B.L., Hu, T., Zhao, H., 1994. The first discovery of *Walchiopremnon gaoi* sp. nov. in China. In: Geological Section of Beijing Graduate School, China University of Mining and Technology (Eds.), Selected papers on coal geology. China Coal Industry Publishing House, Beijing, pp. 118–125 (in Chinese with English abstract).
Traverse, A., 1950. The primary vascular body of *Mesoxylon thompsonii*, a new American cordaitean. American Journal of Botany 37, 318–325.
Vogellehner, D., 1967. *Scalaroxylon multiradiatum* n.g. n. sp. ein Cycadophytina–Sekundärholz aus dem Keuper von Franken. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 128, 215–228.
Walton, J., 1957. On *Protopitys* with a description of a fertile specimen *Protopitys scotica* sp. nov. from the Calciferous sandstone series of Dunbartonshire. Transactions of the Royal Society of Edinburgh 63, 333–340.
Wang, S.J., 1997. A study on origin and evolution of Cordaitaceae in late Palaeozoic. Acta Phytotaxonomica Sinica 35, 303–310 (in Chinese with English abstract).
Wang, S.J., Li, S.S., Hilton, J., Galtier, J., 2003a. A new species of the sphenophyte stem *Arthropitys* from Late Permian volcaniclastic sediments of China. Review of Palaeobotany and Palynology 126, 65–81.
Wang, S.J., Hilton, J., Tian, B.L., Galtier, J., 2003b. Cordaitalean seed plants from the Early Permian of North China. I. Delimitation and reconstruction of the *Shanxioxylon sinense* plant. International Journal of Plant Sciences 164, 89–112.
Wang, S.J., Hilton, J., Liang, M.M., Stevens, L., 2006. Permineralized seed plants from the Upper Permian of southern China: a new species of *Cardiocarpus*. International Journal of Plant Sciences 167, 1247–1257.
Wang, S.J., Sun, K.Q., Cui, J.Z., Ma, S.M., 2009. Fossil plants from coal balls in China. In: Cui, J.Z. (Ed.), Fossil Flora of China. Higher Education Press, Beijing, China.
Wang, H., Shao, L., Hao, L.M., Zhang, P.F., Glasspool, I.J., Wheeley, J.R., Wignall, P.B., Yi, T.S., Zhang, M.Q., Hilton, J., 2011a. Sedimentology and sequence stratigraphy of the Lopingian (Late Permian) coal measures in southwestern China. International Journal of Coal Geology 85, 168–183.
Wang, S.J., He, X.Y., Shao, L.Y., 2011b. Cycad wood from the Lopingian (Late Permian) of Southern China: *Shuichengoxylon tianii* gen. et sp. nov. International Journal of Plant Sciences 172, 725–734.
Whiteside, K.I., 1974. Petrified cordaitean stems from North America. (Ph.D. dissertation) University of Iowa, Iowa City.
Zhang, W., Wang, Y.D., Saiki, K., Li, N., Zheng, S.L., 2006. A structurally preserved Cycad-like stem, *Lioxylon liaoningense* gen. et. sp. nov., from the Middle Jurassic in Western Liaoning, China. Progress in Natural Science 16, 236–248.
Zhao, X.H., Mo, Z.G., Zhang, S.Z., Yao, Z.Q., 1980. Late Permian flora from western Guizhou and eastern Yunnan. In: Nanjing Institute of Geology and Palaeontology, Academia Sinica (Eds.), Late Permian Coal Bearing Strata and Biota From Western Guizhou and Eastern Yunnan. Science Press, Beijing (In Chinese).